

A COMPARISON OF *POA TRACYI* AND *POA OCCIDENTALIS* (POACEAE: POEAE)¹

ROBERT J. SORENG AND STEPHAN L. HATCH

*Department of Biology, New Mexico State University, Las Cruces,
NM 88003, and Department of Range Science, Texas A & M University
College Station, TX 77843.*

ABSTRACT

Poa tracyi and *P. occidentalis* were found to be distinct, but closely related, species. Character differences between the taxa correspond to differences in breeding system, phenology, ecology, distribution, and possibly chromosome number. The species are rarely closely sympatric. Nevertheless, some intergradation and a few intermediate plants are apparent. Stepwise discriminant analysis correctly identified 99% of the 278 specimens tested. Geographic range of *P. tracyi* extends from northern Colorado to south central New Mexico; that of *P. occidentalis* from southwestern Colorado to southern New Mexico, east central Arizona and west Texas. New chromosome number reports are: *P. tracyi* $2n = 28$; *P. occidentalis*, $2n = ca\ 28$ with meiotic irregularities, and; *P. reflexa*, $2n = 28$. A key to *P. tracyi*, *P. occidentalis*, and similar species, *P. leptocoma*, *P. reflexa*, and *P. curta* is included.

INTRODUCTION

Poa tracyi Vasey and *P. occidentalis* Vasey are two closely related species, placed in the Palustres group by Hitchcock (1935), or the Leptocomae by V. L. Marsh (1950). Both are rather uncommon endemics to the mesic regions of the southern Rocky Mountains. A taxonomic problem arises from the morphological similarity of the taxa and the occurrence of intermediates, particularly in south central New Mexico. Marsh (ibid.) and Keck (unpublished typescript), in monographic treatments of the genus, maintained them as distinct species, a conclusion reported by Soreng (1980) and supported here. However, the separation of these taxa has been questioned by other authors. Wootton and Standley (1913), and Hitchcock (1935) doubted *P. tracyi* and *P. occidentalis* were distinct from one another, and as have Martin and Hutchins (1980), indicated that *P. tracyi* was known only from the type locality. Harrington (1954) called all Colorado specimens of these grasses *P. occidentalis* even though *P. tracyi* is actually the more widespread there.

Confused nomenclature, adds to the difficulty of understanding these taxa. Both have been described as *P. occidentalis*. *Poa occidentalis* Vasey was described from the type specimen of *P. trivalis* L. var. *occidentalis* Vasey,

¹ Submitted as Journal Article 968, New Mexico Agric. Exp. Sta., New Mexico State Univ., Las Cruces.

the latter a *nomen nudum*. *Poa tracyi* has a synonym, *P. flexuosa* Muhl. var. *occidentalis* Vasey, that was incorrectly raised to *P. occidentalis* (Vasey) Rydberg. *Poa occidentalis* (Vasey) Rydberg, is the later homonym, and is not synonymous with *P. occidentalis* Vasey. Weber and Johnston (1979), and Dorn (1977), accepting Keck's interpretation for Wyoming (1964), respectively call all Colorado and Wyoming material *P. tracyi*. However, they submerge *P. occidentalis* Vasey rather than *P. occidentalis* (Vasey) Rydberg under *P. tracyi*. This is the reverse of what Keck had done. Rydberg had published different names and synonymies for these species before he finally sorted this out in 1922.

In addition to nomenclatural confusion and morphological similarity between the taxa, their geographical distributions have been wrongly reported. *Poa occidentalis* Vasey has been reported from the Pacific States, Alaska, Utah, Wyoming, and western Canada, *Poa tracyi* from Montana, Idaho, Utah, and Wyoming apparently all on misapplications of these names. This and the long-term (and continuing) disparity over the taxonomic treatment of these taxa, led us to undertake this study.

MATERIALS AND METHODS

Poa occidentalis and *P. tracyi* were morphologically compared using samples from the region of geographic overlap between the taxa, and herbarium specimens from 23 herbaria. The results were combined with other biological data, to evaluate their taxonomic relationship. Population samples, observation on anthesis, and habitat data comes primarily from field work in the summers of 1978 through 1982, including 23 and nine different extensive collections of *P. occidentalis* and *P. tracyi* respectively. Some information on habitat was gleaned from specimen labels and floristic works. All voucher specimens are housed at NMC unless otherwise indicated.

Our sample for statistical analysis, after eliminating duplicate, incomplete, and immature specimens, include 23 *P. occidentalis* and 28 *P. tracyi* herbarium specimens, and 102 *P. occidentalis* and 125 *P. tracyi* population specimens. The four *P. occidentalis* populations used in discriminant analysis represent most of the geographic range of this species. Six populations of *P. tracyi* were used from the same general region. Collection locations are cited in Table 1, and are illustrated in Fig. 1.

Twenty-six morphological characters (Table 2) were measured and ranked in the following manner: Leaf sheath scabrosity, and ligule pubescence, 0 = absent, 1 = scant, or 2 = abundant; percent leaf sheath closure, 0 = 0-9%, 1 = 10-19%, 2 = 20-29% closed, etc.; lemma intermediate nerve distinctness, and between-nerve pubescence, 0 = faint or absent, or 1 = distinct; inflorescence emergence from the upper leaf sheath, 0 = lowest inflorescence node exerted more than 5 cm, 1 = lowest node exerted less than 5 cm, 2 = lowest node enclosed; and, portion of lemma keel and marginal nerve covered by pubescence as closest to, 0 = 0%, 1 = 25%,

TABLE 1. Collection locations of the population samples used in the comparison of *Poa occidentalis* and *P. tracyi*. N = the number of individuals examined in each population.

Poa occidentalis Vasey (4 populations). NEW MEXICO. Otero Co.: Sacramento Mts., Benson Ridge, 3 Aug 1979, *Soreng* 464 (N = 30). Bernalillo Co.: Sandia Mts., Dry Camp G.G., 14 Aug 1978, *Soreng & Hatch* 1 (N = 8). Santa Fe Co.: Sangre De Cristo Mts., ca 1 km S of Big Tesuque C.G. along Hyde Park Rd., 15 Aug 1978, *Soreng & Hatch* 10 (N = 27). Rio Arriba Co.: San Juan Mts., Rio Puerco C.G., 16 Aug 1978, *Soreng & Hatch* 48 (N = 29).

Poa tracyi Vasey (6 populations). NEW MEXICO. Lincoln Co.: White Mts., below Sierra Blanca Peak, 8 Aug 1979, *Soreng & Smith* 530 (N = 35). Bernalillo Co.: Sandia Mts., Sandia Crest N of tram, 16 Jul 1981, *Soreng & Gadzia* 1642 (N = 15). Colfax Co.: canyon N of Raton City Park, 11 Aug 1978, *Soreng & Hatch* 64 (N = 23); Raton Pass, on side on Bartlet Mesa, 22 Jul 1979, *Soreng* 385 (N = 28); ca 12 km NW of Raton, on the Raton Ranch, 25 Jul 1979, *Soreng* 401 (N = 22). Colorado. Huerfano Co.: E slope of the Sangre de Cristo Mts., Trinchera Peaks area, ca 8 km W of Cucharas Pass, 21 Jul 1979, *Soreng* 381 (N = 7).

2 = 33%, 3 = 50%, 4 = 66%, and 5 = 75%. The remaining characters were continuous except for number of branches at the lowest inflorescence node, number of florets per spikelet, and number of spikelets per longest branch. Seven more characters were generated by taking ratios of some of the continuous characters (Table 2).

The existence of two taxa was supported by differences between them in several characters states, particularly anther length. However, since some species have both long-anthered out-crossing populations and short-anthered inbreeding ones, additional evidence was needed. Therefore, phenology, breeding system, ecological data, and chromosome number were examined. Date of anthesis was estimated to the nearest month from 72 different collections. For 58 of these with exact dates of collection, more precise estimates were made to an early, mid, or late month date. All dates were used to study flowering time over the latitudinal range of each species. Only the more precise estimates were used to examine the overlap of flowering periods.

Differences in breeding system between the taxa were estimated by examining anther lengths, degree of floret openness, stigma exposure, and anther exertion from the floret on collected specimens in anthesis. All flowers had pistils. A plant was classified as perfect (at least in part) if at least one flower was found with developed anthers. If all the anthers on a plant were vestigial (i.e., obviously aborted), or absent, the plant was considered imperfect. Observations were also made on plants in the field and in a garden.

For chromosome data, meiotic material was fixed in ethanol-acetic acid (3:1), or ethanol-chloroform-acetic acid (4:3:1), and stained in alcoholic-hydrochloric acid carmine (Snow, 1963), or acetocarmine, and squashed in

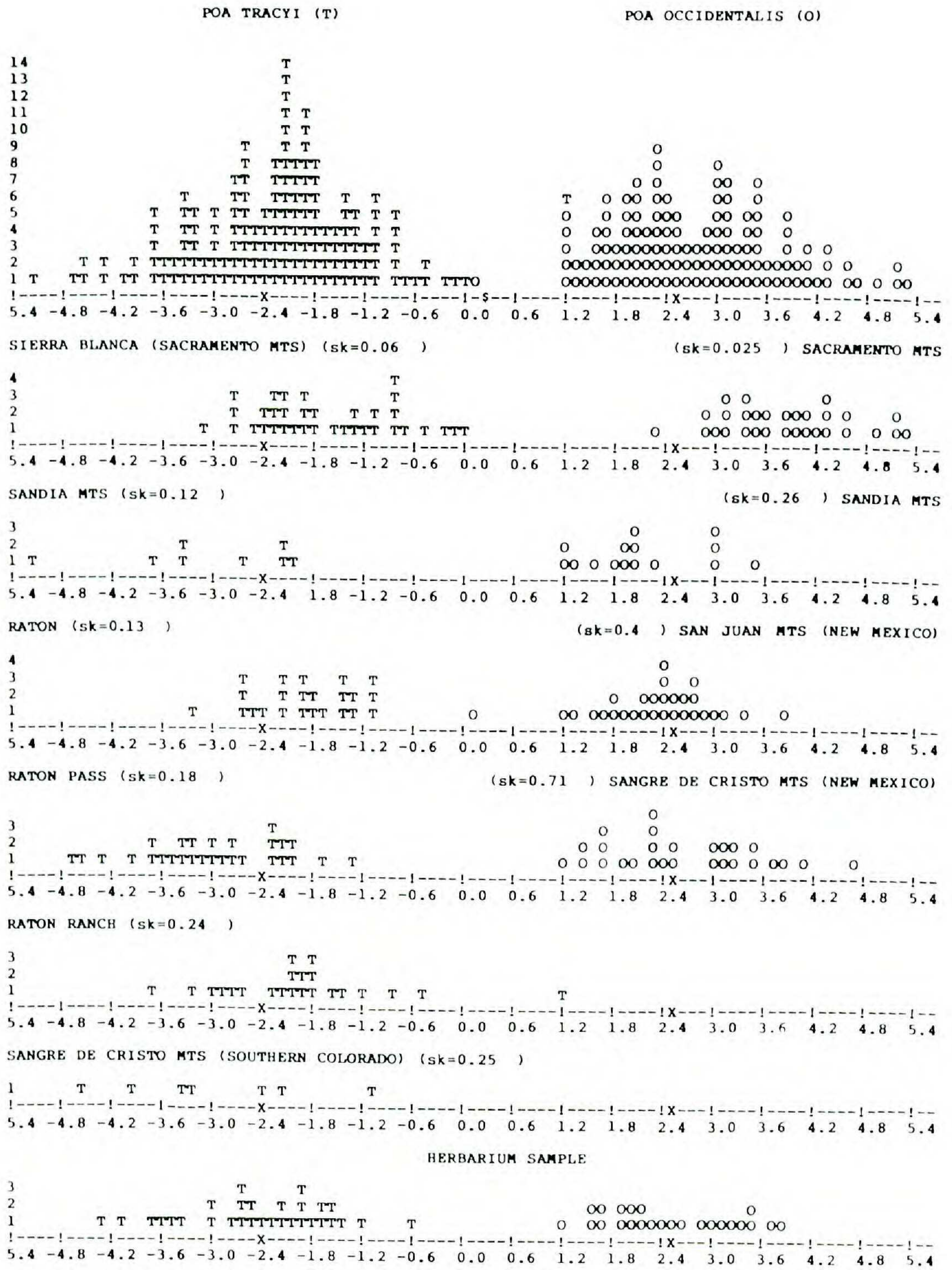


Figure 1. Histogram of the canonical variable for the separation of *Poa tracyi* and *P. occidentalis*. Population samples are indicated according to their site of collection. Each line compares populations of the two species from approximately the same latitude. X's indicate the means of the herbarium samples and *sk* the deviation from the mean of a species. The vertical axis is frequency. The dividing point between the species, as selected by the CVA, is indicated by a \$ on the first horizontal axis.

a standard manner. Root tips were fixed and examined in a standard manner. The only chromosome number previously known for either species was $2n = 14$ for *P. occidentalis* (Hatch, 1980).

After it became evident that two morphologically and biologically distinct taxa were present, the data were submitted to the BMDP7M stepwise discriminant analysis (SDA) program (Dixon, 1975). This program also performs a modified canonical variates analysis (CVA) using the characters selected in the SDA. The SDA stepping process cut off level was an F-value of at least four to enter another character. Statistical distributions were examined for each character using Statistical Analysis Systems (SAS) (Barr et al., 1976) for basic statistics, character correlation matrices, and histograms. Only measured single characters appearing to have normal distributions were used in the SDA. Anther characters were used apriori to divide the groups for the SDA. However, anther-length was omitted in the analysis because in *P. tracyi* anthers may be either short and aborted or long and fertile.

RESULTS

MORPHOLOGY. *Poa occidentalis* and *P. tracyi* not only have a very similar aspect but broadly overlap in most of the continuous characters measured (Table 2). The characteristics of sheath scabrousness and panicle breadth, by which Hitchcock (1935) distinguishes these taxa, are not satisfactory to separate them. However, these taxa can be readily distinguished by a suite of characters which when considered together will separate nearly every individual. This suite of characters in turn corresponds to differences in phenology, breeding system, and habitat. In addition to anther length (the only character that does not overlap between these taxa), the most consistent discriminators are the openness of sheaths, and the ligule length-leaf blade width ratio. Some less constant features distinguishing them are the presence in *P. occidentalis* of more spikelets crowded on the branches, florets that are relatively smaller and less pubescent, and very scabrous sheaths. These features did not change when the taxa were grown in a common garden.

PHENOLOGY. The morphological distinction between the taxa corresponds to differences in flowering times. Flowering times for both taxa barely overlap locally (fig. 1), and generally become progressively later from north to south (fig. 2). *Poa tracyi* in south central New Mexico is an exception by flowering into mid-August, a fact probably significant in understanding the morphological variability of the species there. When *P. tracyi* from Raton, and *P. occidentalis* from Cloudcroft, New Mexico, were grown together in Las Cruces, New Mexico (a garden 610 m lower than their known elevational ranges), they flowered in May and June respectively, still maintaining a full month separation. Observation of these taxa in the field and garden reveals that plants flower over a short duration

TABLE 2. Means, standard deviations, ranges, and F values from tests of equality of means for characters used in the comparison of *Poa tracyi* and *P. occidentalis*. All metric character expressions are in mm. The first 12 characters are listed in the order in which they were selected in the stepwise discriminant analysis ($df = 1, 278$), the remaining characters have $df = 1, 293$. Significance for F values is indicated as follows: NS = $P > 0.1$; * = $P < 0.1$; ** = $P < 0.05$; *** = $P < 0.01$; blank = $P < 0.005$.

Character	POA TRACYI		POA OCCIDENTALIS		F-value
	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range	
Sheath % closed	62±3.3	(0-9)-(80-89)	36±0.8	(20-29)-(50-59)	532
Palea length	3.0±0.4	2.0-4.1	2.5±0.3	1.7-4.0	167
Second glume length	3.2±0.5	2.2-4.9	3.3±0.4	2.6-4.6	9.5
Ligule length	2.0±0.7	0.4-4.5	3.6±1.4	1.0-12.2	148
Leaf blade length	115.7±30.6	30-229	105.1±30.0	35-180	9.3
First lemma length	3.8±0.5	2.6-5.0	3.4±0.4	2.6-4.9	68
Lemma keel pubescence	58±0.7	(0-20)-(75-90)	48±0.6	(0-20)-(75-90)	53
Leaf blade width	3.3±0.9	1.5-5.6	2.9±1.2	1.2-12.3	13
Florets per spikelet	3.2±1.1	1-5	4.7±1.0	1-7	24
Spikelet length	5.1±1.0	2.9-8.1	4.7±0.9	3.0-8.0	NS 1.8
Spikelets per longest branch	12.8±5.3	3-35	34.2±22.0	4-120	136
First glume	2.6±0.4	1.6-3.5	2.8±0.3	1.7-3.7	14
Inflorescence length	187±40	80-283	198±61	61-391	NS 0.5
Inflorescence width	87±33	18-206	90±53	13-265	NS 0.9
Inflorescence longest branch	80±23	23-184	108±37	27-227	56
Inflorescence # of branches at lowest node	2.8±0.8	1-5	3.1±1.1	1-7	** 4.8
Inflorescence elongation	0.3±0.5	0-3	1.1±0.8	0-3	122
Plant height	691±163	320-1245	549±201	196-1115	52
Leaf sheath scabrosity	0.3±0.5	0-2	1.7±0.5	0-2	519
Leaf sheath length	103±19	57-142	94±32	38-194	*** 7.1
Leaf total length	218±42	107-318	199±57	73-338	9.0
Ligule pubescence	1.1±0.7	0-2	1.8±0.5	0-2	96
Lemma marginal nerve pubescence	38±0.8	(10-20)-(75-85)	30±0.7	(10-20)-(75-85)	65

Lemma between nerve pubescence	0.9±0.3	0-1	0.4±0.5	0-1	92
Distinctness of lemma intermediate nerve	0.4±0.5	0-1	0.8±0.4	0-1	46
Anther length (developed)	2.2±0.4	1.2-3.0	0.6±0.1	0.4-1.0	—
Plant sex	0.6±0.5	0-1	1.0±0.0	1-1	75

RATIOS

Panicle length/ Plant height	28%±7.3	16%-73%	37%±6.1	22%-59%	NS 0.6
Blade length/ Sheath length	114%±29	39%-260%	117%±28	56%-228%	NS 0.9
Ligule length/ Blade width	64%±21	8.8%-146%	127%±33	56%-227%	422
Palea length/ Lemma length	80%±7.7	58%-107%	73%±5.7	51%-94%	—
First glume/ First lemma	69%±9.2		83%±7.2		205
Second glume/ First lemma	83%±9.1		99%±7.4		255
Spikelet no. on/ Longest branch	16%±6.1		31%±13.2		157

(2-3 weeks), seeds mature, and plants do not normally produce reproductive shoots again during that season. A notable exception is *P. tracyi* from Clear Creek Co., Colorado, dated August (*Walker s.n.*), having a tiller in anthesis.

ASPECTS OF BREEDING SYSTEM. The apparent breeding behavior of these taxa supports the morphological and phenological distinctions between them. Four observations lead to the conclusion that the taxa have different breeding systems. 1) Differences in anther length and corresponding numbers of pollen grains: *Poa occidentalis* anthers range from 0.3-1 mm (mean 0.6 mm) in length. Fertile anthers of *P. tracyi* range from 1.25-3 mm (mean 2.2 mm) in length. Thus, *P. tracyi* anthers average four times the length of *P. occidentalis* anthers, a ratio that corresponds to the average numbers of pollen grains in their flowers (3000:600). 2) Deviations from wholly hermaphroditic flowers: Of 143 *P. tracyi* specimens 66% were perfect at least in part, 9% were estimated to be pistillate, lacking even vestigial anthers, and 25% were pistillate but had vestigial anthers. Thus, *P. tracyi* is partially gynodioecious. Abortive anthers were not found in *P. occidentalis*. 3) Variation in flower activity at anthesis: Florets of *Poa occidentalis* rarely open during anthesis. Pollen is abundant inside the florets, and their small stigmas are rarely even shortly exerted. The dehisced anther sacs of this taxon, only slightly protruding from mature florets, appear to have been pushed out by developing caryopses. In contrast, florets in *P. tracyi* mostly

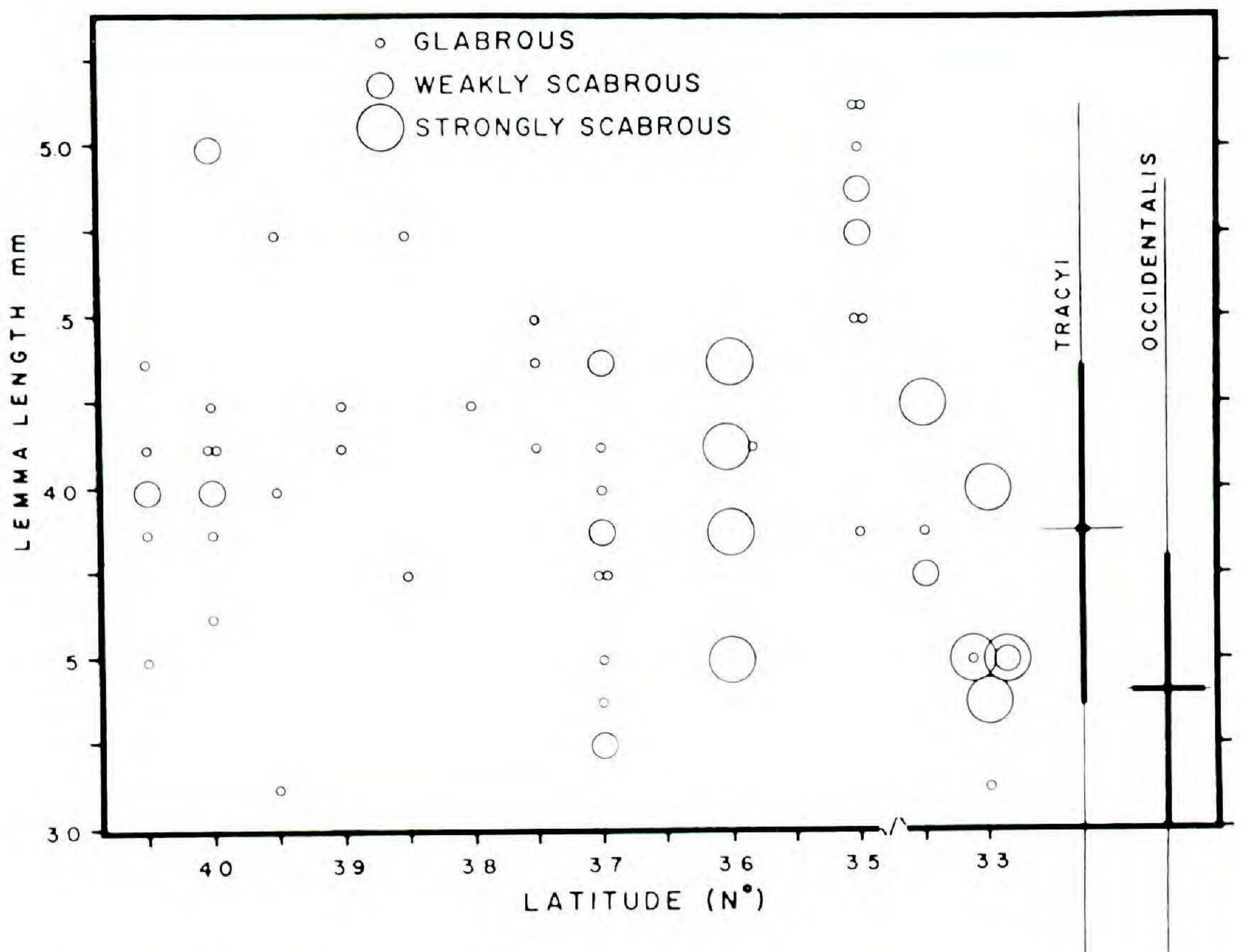


Figure 2. Plot of first lemma length and sheath scabrousness against latitude of occurrence for *Poa tracyi*. The figures at the right are mean, standard deviation, and range for first lemma lengths (vertical), and mean, and range of sheath scabrousness (horizontal). 40.5° N is approximately the northern border of Colorado: 37° N is approximately the Colorado-New Mexico border: 33.5° represents collections from the White Mts. N. M.: 33° represents collections from the Sacramento Mts. N. M.

are widely open at anthesis, with anthers mostly completely exerted and relatively large stigmas well exposed. 4) Differences in habitat tolerance: *Poa occidentalis* is mostly autogamous, and autogamous species are more often associated with early successional habitats than are xenogamous ones (Cruden 1977). Sixteen of 23 sites where we collected *P. occidentalis* were highly disturbed. This finding may be biased because disturbed areas by their nature are more easily accessible, but in contrast we only found *P. tracyi* in relatively undisturbed habitats (nine collections). Garden and field studies indicate that the differences between these taxa in the above characteristics are primarily genetic.

CHROMOSOME NUMBERS. *Poa tracyi* was consistently tetraploid ($2n = 28$) in five different plants from four different locations around Raton, New Mexico. No irregularities were found in meiosis. Indications are that *P. occidentalis* is diploid with $2n = 14$ (Hatch, 1980), and $n = ca 7$. However, a third plant (*Soreng 123-b*), $2n = ca 28$, may have been autotetraploid. It greatly exceeded the dimensions of neighboring plants being over

1 m tall and having leafblades more than 1 cm wide, but was similar in all other features. Although the chromosome preparation was poor there appeared to be many quadrivalents. Other species in this complex are *P. leptocoma* Trin. seven counts $2n = 42$, including two counts reported here (Cave, 1964; Fedorov, 1969; Moore, 1973 and 1977; Goldblatt, 1981), and *Poa reflexa* Vasey & Scribn. $2n = 28$, three new counts. The chromosomes of *P. curta sensu auct.* have not been counted. See Table 3 for collection citations.

STEPWISE DISCRIMINANT ANALYSIS. We used stepwise discriminant analysis (SDA) to test the distinctness of the two recognized taxa. The resultant SDA model (Table 4), based on 12 characters, correctly identified 276 out of 278 (99%) of the specimens. A "classification function" using these characters is presented in Table 4, and any future individual of *P. occidentalis* or *P. tracyi* may be identified with this. The most potent characters for discriminating between the taxa were the combination of percent sheath openness, palea length, and second glume length. The two misidentified specimens were members of sampled populations that otherwise showed no intermediacy between the taxa. These specimens are easily recognized as members of their respective taxa by characteristics (including anther length) not included in the SDA model.

A single linear canonical variable was calculated using the 12 SDA characters in a modified canonical variates analysis (coefficients are listed in Table 4). With this variable, each individual was projected onto a line where the group means were separated as far as possible. The resulting histogram (fig. 3) shows a clear distinction between the taxa. To examine the relative position of each population in this plot, values from individual populations were projected below their parent taxon (fig. 3). Assuming that the means of the herbarium samples were the best available estimates of the taxa means, we attempted to measure how far each population sample deviated from the mean of its taxon. By summing the scalar deviations of individuals above (sk_1) and below (sk_2) the taxon mean for each population, and then dividing the smaller deviation by the larger one,

$$\begin{aligned} sk_1 &= (X_i - \bar{X}) \text{ for } X_i < \bar{X} \\ sk_2 &= (X_i - \bar{X}) \text{ for } X_i > \bar{X} \end{aligned}$$

a skewness (sk) value was obtained that was between 1 (= centered on the mean) and 0 (all values on one side of the mean). In *P. tracyi*, the Sierra Blanca (White Mts.) sample ($sk = 0.06$), collected in close proximity to *P. occidentalis*, was the most strongly skewed from its species mean toward the other taxon. However, the Sacramento Mts. population of *P. occidentalis* is even more strongly skewed from its mean, away from *P. tracyi*. Although the positions of the other samples fluctuated about the taxon means when different character sets were used in this procedure, the above two populations retained their relative positions.

TABLE 3. Cytological vouchers.

POA OCCIDENTALIS: $2n = 14$, NEW MEXICO. Otero Co.: Cloudcroft, *Hatch* 2222 (TAES); $2n$ ca 28, 11 km NE of Cloudcroft, Dec 1978, *Soreng* 123-b; $n = 7$, Rio Arriba Co.: ca 33 km NW of Los Alamos, 15 Aug 1978, *Soreng & Hatch* 48.

POA TRACYI: $2n = 28$, NEW MEXICO. Colfax Co.: canyon N of Raton City Park, 11 Aug 1978, *Soreng & Hatch* 64, and 31 May 1979, *Soreng* 266; Raton Pass, on side on Bartlet Mesa, 1 June 1979, *Soreng* 267; ca 12 km NW of Raton, on the Raton Ranch, 3 Jun 1979, *Soreng* 274, and 7.5 km NW of Raton, *Soreng* 272.

POA REFLEXA: $2n = 28$, WYOMING. Sublette Co.: ca 50 km due N of Pinedale, Little Sheep Mt., 10 Aug 1980, *Soreng & Spellenberg* 1260. UTAH. Summit Co.: ca 80 km due E of Salt Lake City, Bald Mt., 11 Aug 1980, *Soreng & Spellenberg* 1336. NEW MEXICO. Taos Co.: Wheeler Peak, in La Cal Basin, 19 Aug 1980, *Soreng & Spellenberg* 1478.

POA LEPTOCOMA $2n = 42$, CANADA. Banff Natl. Park, E slopes of Mt. Peyto, 28 Jul 1980, *Soreng & Spellenberg* 1016. MONTANA. Glacier Natl. Park, 5 km NE of Logan Pass, 4 Aug 1980, *Soreng & Spellenberg* 1148.

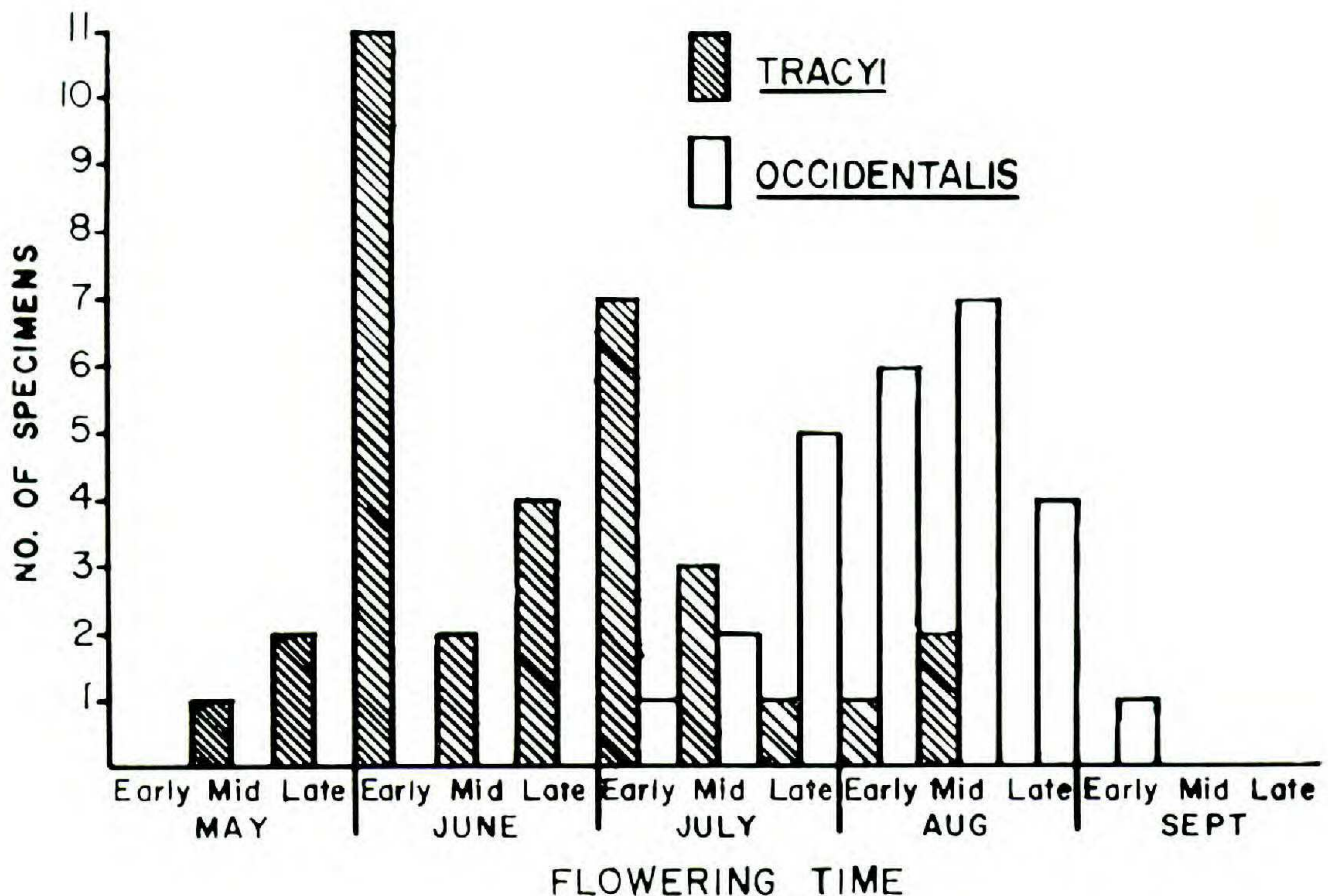


Figure 3. Histogram of the flowering times of *Poa tracyi* and *P. occidentalis*.

DISCUSSION

Comparison of *Poa occidentalis* and *P. tracyi* populations from the region of geographic overlap, and from herbarium specimens collected throughout their ranges, revealed two morphologically distinct groups. These groups in turn correspond to differences in phenology, certain aspects of breeding system, and possibly chromosome number. A stepwise discriminant analysis correctly identified 99% of the specimens tested. The additional character of anther length, or the presence of aborted anthers, was sufficient to distinguish all mature plants of these taxa.

The geographic distributions (fig. 2) of *P. occidentalis* and *P. tracyi* apparently do not overlap in Colorado. However, in New Mexico the taxa both occur in the San Juan, Sangre De Cristo, Sandia, White, and Sacramento mountains. The taxa are rarely sympatric, and remain morphologically distinct except in a few specimens from the Sangre De Cristo and Sacramento mountains. These specimens exhibit a mix of characters that normally distinguish only one or the other taxon. In addition, *P. tracyi* seems to have gained some characteristics of *P. occidentalis* in south central New Mexico.

Poa tracyi from the White and Sacramento mountains is morphologically highly variable. Specimens from there range from being nearly identical to type material of *P. tracyi* (from Raton area), to a few specimens that are difficult to distinguish from *P. occidentalis* except by anther length. One specimen (*Hitchcock* 13303; US) combines characters from both taxa and might best be considered a hybrid. In this region *P. tracyi* often has smaller spikelets, and very scabrous (occasionally pubescent) sheaths (six herbarium specimens and part of our Sierra Blanca population sample). Figure 4 illustrates this shift. In addition, in the Sangre De Cristo Mts. two collections of *P. tracyi* exhibit densely scabrous sheaths, one (*Standley* 4344; NMC, US) is possibly a hybrid. Other workers have noted the scabrouness of *P. tracyi* in the Sacramento Mts. Keck (unpublished) named a subspecies of *P. tracyi* based on sheath scabrousness in this region. A. S. Hitchcock, in his collection notes from there (August, 1915), correctly determined several specimens as *P. tracyi* and others as *P. occidentalis*. However, because his key character of sheath scabrosity breaks down there, he subsequently reclassified all his *P. tracyi* specimens from there as *P. occidentalis*. He later expressed his doubts about the distinctness of *P. tracyi* (*Hitchcock* 1935). However, in contrast to the variability of *P. tracyi*, *P. occidentalis* plants from the White and Sacramento mountains do not exhibit any tendency toward *P. tracyi*, and, as seen in the CVA histogram, may even deviate from the mean of *P. occidentalis* and away from *P. tracyi*. The simplest and most satisfactory explanation for these characters shifts in *P. tracyi* toward *P. occidentalis*, and the intermediacy seen between them appears to be introgression of *P. occidentalis* genes into *P. tracyi*.

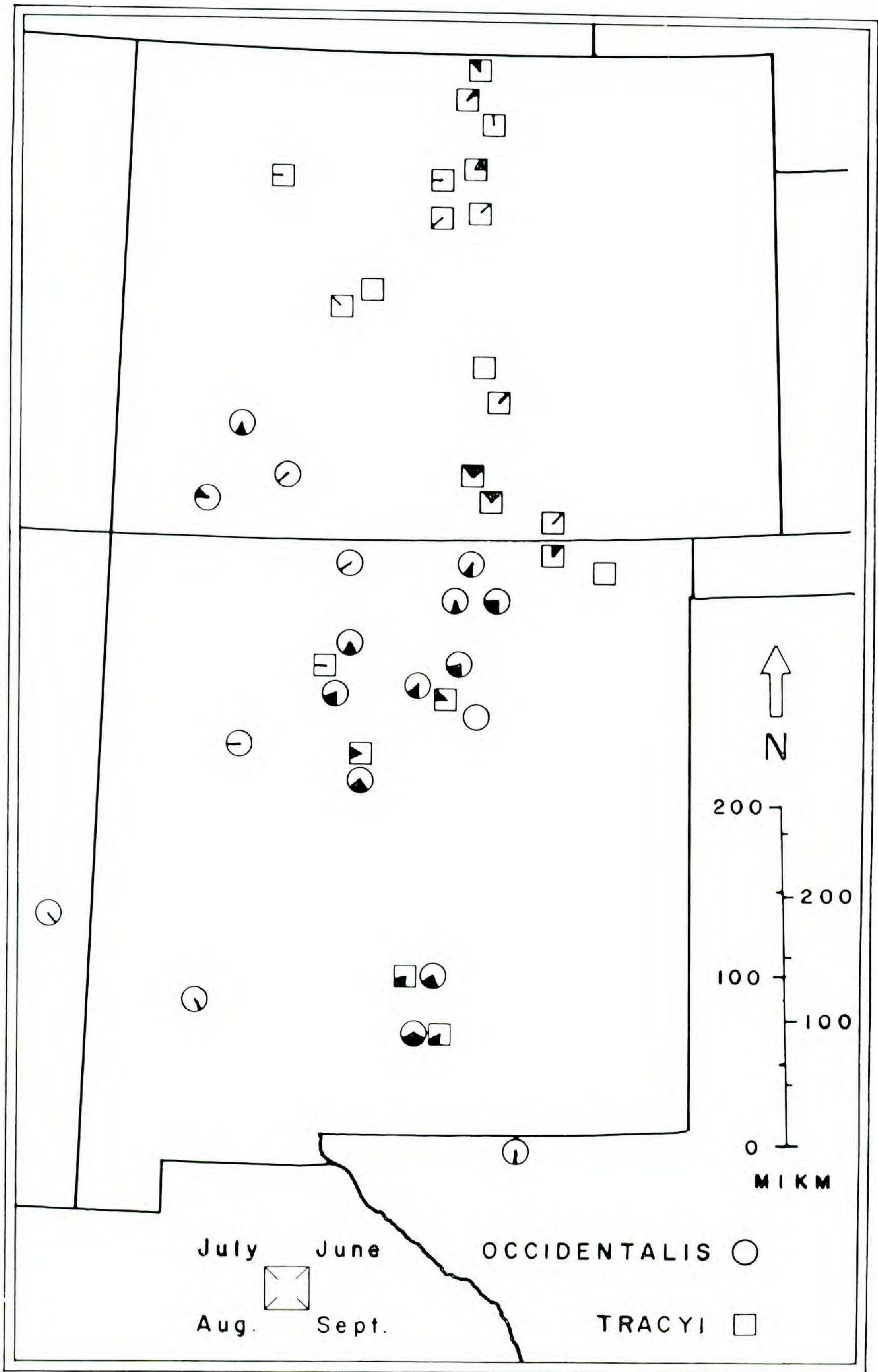


Figure 4. Geographical ranges and flowering time distributions through the ranges of *Poa tracyi* and *P. occidentalis*.

TABLE 4. SDA "classification function" and canonical variable coefficients.

Character	Classification function		Canonical Variable
	<i>P. tracyi</i>	<i>P. occidentalis</i>	
% Sheath closure	7.46839	4.08081	-0.67465
Palea length	1.88443	0.69584	-0.09730
Second glume length	-0.14802	0.53967	0.13696
Ligule length	-0.29283	0.03698	0.06568
Leafblade length	0.14021	0.08170	-0.01165
First lemma length	1.87414	1.08741	-0.15668
Lemma keel pubescence	8.98786	7.20448	-0.35516
Leafblade width	0.08673	-0.17177	-0.05148
Florets per spikelet	-4.48858	-2.66681	0.36281
Spikelet length	0.27300	0.15623	-0.02326
Spikelets per longest branch	0.08221	0.15108	0.01374
First glume length	0.31108	0.73634	0.08469
Constant	-91.51909	-58.86263	6.61007

CONCLUSIONS

A situation where two related taxa grow sympatrically without hybridizing is often considered the best possible evidence for distinct species (Mayr, 1969, p. 195). In *P. occidentalis* and *P. tracyi*, hints of introgression and the presence of putative hybrids from a few locations, indicate that a test of sympatry has failed occasionally. However, the distinctive biology of these taxa, and the ease of distinguishing the vast majority specimens, should outweigh possible limited hybridization. Furthermore, these taxa are diploid, or low polyploid, and are narrow in distribution. No diploid apomicts are known in the Poaceae. These points seem central to arguments delimiting species in *Poa* or any taxonomic group in which extensive hybridization and high polyploidy combine with apomixis to obscure specific differences. We doubt that *P. tracyi* has arisen as a direct autopolyploid from *P. occidentalis*. They are morphologically too distinct. In all probability, if *P. tracyi* is of hybrid origin, *P. occidentalis* may be one of its parents, or, if it is an autotetraploid, then it may have come from some common ancestor in the complex which has since disappeared. Hence, we must conclude that they are two species, and possibly better than most in *Poa*.

TAXONOMY

The species in the complex referred to earlier in this paper are all endemic to (except *P. leptocoma*) the central and southern Rocky Mountains, and the mountains of the Colorado Plateau. *Poa tracyi*, *P. occidentalis*, *P. reflexa*, *P. leptocoma*, and *P. curta* seem to form a closely related group. Known chromosome numbers were added to the key as an indication of the present level of knowledge.

KEY TO THE SPECIES

1. Anthers over 1.25 mm long, averaging more than 2 mm, (often aborted in *P. tracyi*); sheaths usually closed $\frac{1}{2}$ their length or more; plants often short-rhizomatous; usually few-flowered; rich soil in forest openings to subalpine habitats.
2. Lemmas prominently pubescent on the keel and marginal nerves, usually sparsely so between them, with long cobwebby hairs from the callus; ligules often puberulent abaxially; primarily in the front ranges of CO and NM; $2n = 28$ *P. tracyi*
2. Lemmas glabrous or nearly so, rarely sparsely puberulous, without long hairs on the callus; sheaths and ligules glabrous or nearly so; leaves broad and short; UT reaching sw. ID, and w. WY?..... *P. curta sensu auct.*
1. Anthers 1 mm long or less, flowers without abortive anthers; sheaths usually open $\frac{1}{2}$ their length or more; plants not at all rhizomatous (occasionally so in *P. leptocoma* and then of wet habitats); other characters variable.
3. Sheaths more or less densely retrorse-scabrous, infrequently glabrous; lemmas narrow, 2.6—4.9 mm long, with a scarious, white apex, this rarely at all bronze tinged; ligules mostly scabrous abaxially; culms to 110 cm tall; panicles (6—) 12—40 cm long; palea nerves glabrous, rarely sparsely ciliate; plants of mesic forested habitats, at elevations under 3500 m, from s. CO to s. NM, w. TX, and e.cent. AZ; $2n = 14$ (28)..... *P. occidentalis*
3. Sheaths sparsely retrorse-scabrous, to roughened or glabrous; lemmas broadly lanceolate and acute, or narrow and sharply acuminate, but if narrow then with the apical scarious portion bronze tinged; ligules smooth; palea nerves usually pubescent; plants usually of mesic, high mountain forests, or alpine habitats, rarely below 3300 m elevation if in the range of *P. occidentalis*.
4. Palea keels pilose-pubescent, (this sometimes obscure even under 25X); floral bracts broadly lanceolate, the glumes nearly equal; lemmas abundantly pubescent on the nerves, the intermediate nerves often distinct, sometimes pubescent; leaf blades usually short, broad, and strongly keeled; plants of mesic to wet habitats; in the Rocky Mts. from cent. Montana to n. NM, rare w. of UT; $2n = 28$ *P. reflexa*
4. Palea keels with antrorsely curved cilia or glabrous (under 25X); floral bracts long and narrow, sharply acuminate, the first glume often much shorter than the second and very narrow; lemmas often purplish, usually bronze-tinged at the apex, sparsely pubescent on the nerves, glabrous between them, the intermediate nerves usually obscure; leaf blades usually long, narrow, lax, and weakly keeled; plants of wet habitats; boreal, e. Russia, w. North America, to s.cent. NM; $2n = 42$ *P. leptocoma*

POA OCCIDENTALIS Vasey, Contr. U. S. Natl. Herb. 1:274. 1893.

TYPE: NEW MEXICO. Las Vegas, G. R. Vasey s.n., in 1881. Described from the type specimen of *P. trivialis* L. var. *occidentalis* Vasey, 1885 a *nomem nudum*, Descr. Cat. Grasses U.S. 85. (HOLOTYPE: US 79610!).

Poa platyphylla Nash & Rydberg, Bull. Torrey Bot. Club. 28:266. 1901. Based on *P. occidentalis* Vasey, 1893.

Perennial, commonly blue-green and variously anthocyanic, non-rhizomatous, or rarely appearing so; culms often decumbent at the base, erect, to 110 cm tall, glabrous except for some retrorse scabrosity about the nodes; sheaths mostly longer than the internodes, rarely closed more than 50% of their length, strongly keeled, mostly strongly retrorsely scabrous,

rarely glabrous; ligules acute to acuminate, mostly entire, the apices often doubled back on themselves, usually with retrorse spicules on the abaxial surface, those of the upper leaves to 12.2 mm long, usually longer than the leaf width; blades mostly cauline, strongly keeled, flat to folded, prominently prow-tipped, the upper ones usually the longest, 4–18 cm long, 1.2–5.5 mm wide; panicle broadly pyramidal, (6-) 12–40 cm long, nodding with loosely ascending branches when young, erect with widely spreading branches when mature, the longest (3-) 5–23 cm long, with 8–120 spikelets; spikelets oblong, mostly crowded on the distal 1/2 of the branches, 3–8 mm long, with 1–7 florets, usually longer than the subtending pedicel, the rachilla often hidden by the florets; glumes nearly equal, the first 1-nerved, narrow, sharply acute, 2–3.2 mm long, the second 1–3-nerved, broader than the first, broadest at about the lower 1/3, gradually tapered to an acute tip, 2.5–4.2 mm long, nearly equaling the first lemma; lemmas usually green, strongly keeled, with scarious acutish tips that are white or rarely slightly bronzed when the body of the lemma is anthocyanic, the first 2.6–4.2 mm long, with sparse long cobwebby hairs from the callus, villous on the lower 1/2 of the keel, and lower 1/3 of the marginal nerves, glabrous to sparsely puberulent between them, the intermediate nerve usually distinct; paleas glabrous or rarely minutely scabrous on the nerves, 1/2 to nearly equaling the lemma in length; flowers perfect, the anthers 0.3–1.0 mm long.

Southern Rocky Mts., in the San Juan Mts. of SW Colorado, San Juan, Sangre De Cristo, Sandia, White and Sacramento mountains, Mt. Taylor, and the Black Range of New Mexico, White Mts. of Arizona, and the Guadalupe Mts. of Texas. Flowering from (early?) mid-July to September. On generally cool exposures in sparsely vegetated, disturbed and natural forest openings, elevation 2300 to 3500 m.

This species has been reported in floras of Alaska (Hulten, 1968), Canada (Scoggan, 1978), Oregon (Howell, 1903), and California (Abrams, 1940). Most of the reports of *P. occidentalis* occurring other than in the Southern Rocky Mtns. appear to stem from Vasey's unpublished *P. alsodes* Gray var. *occidentalis* which was realized later to be equivalent to *P. laxiflora* Buckl. However, before this realization, this variety was raised to a species as *P. occidentalis* Vasey & Scribn., published by Howell (loc. cit.), perpetuated by Abrams (loc. cit.), and said to be part of the Rocky Mtn. species as well. We examined most of the specimens identified as *P. occidentalis* from these ranges and they are referable to other species. The specimens cited by Scoggan (loc. cit.) as Canadian records could not be located, but are unlikely to be *P. occidentalis* Vasey.

Poa occidentalis was reported from Arizona (McLaughlin & Mason, 1977) based on *McLaughlin* 1217 a collection we believe represents *P. leptocoma*. A new collection (Apache Co.: White Mts. near Black River, N part of T5N, R27E, 6 Sep 1980, *Spellenberg & Soreng* 5248 (ARIZ, NMC)) is the first valid Arizona record of *P. occidentalis*. So far as we know the only record of

Poa occidentalis from Texas is unpublished, but the species has been found there (Culberson Co.: Guadalupe Mts. Nat. Park, elev. 7,700 ft, 14 Aug 1976, Burgess 4284 ARIZ).

Small specimens of *P. occidentalis* are often difficult to distinguish from *P. leptocoma* or *P. reflexa*, which share with it many of the characters that distinguish *P. occidentalis* from *P. tracyi*. These species are normally separated from *P. occidentalis* by their shorter panicles, palea nerve vestiture, lemma coloration (bronze-tinged lemma tips in *P. leptocoma*), and occurrence in more mesic habitats.

POA TRACYI Vasey, Bull. Torrey Bot. Club. 15:49. 1888.

TYPE: NEW MEXICO. Mesa side near Raton, alt. 7000–8000 ft, S. M. Tracy s.n., 1887. (LECTOTYPE: US 556764! (no one specimen in the series was singled out by Vasey); ISOTYPES: CAS!, GH!, NY!, RM!, TAES!, US!). (Jun 10 presumably the correct date of collection. Jul 20, and Jul 10 and 20 dates evidently copying errors, see Tracy, 1888).

Poa flexuosa Muhl. var. *occidentalis* Vasey, in Rothrock in Wheeler, U.S. Survey W. 100th Merid. Rpt. 6:290. 1878. TYPE: COLORADO. Twin Lakes, J. Wolf 1132, in 1873. (LECTOTYPE: US 79768! (no one specimen in the series singled out by Vasey); ISOTYPES: GH!, NY!)

Poa flexuosa Muhl. var. *robusta* Vasey, Contr. U.S. Natl. Herb. 1:271. 1893. TYPE: COLORADO. Bear Cr., latitude 40–41 N, alt. 8000–9000 ft., Vasey 673, in 1968 (Powell's expedition). (LECTOTYPE: US 79767! (no one specimen in the series singled out by Vasey); ISOTYPE: GH-).

Poa autumnalis Muhl. ex. Ell. var. *robusta* (Vasey) Beal, Grasses of North America. 2:534. 1886. Based on *P. flexuosa* var. *robusta* Vasey, 1893.

Poa nervosa (Hook) Vasey var. *tracyi* (Vasey) Beal, Grasses of North America. 2:538. 1896. Based on *P. tracyi* Vasey, 1893.

Poa occidentalis (Vasey) Rydberg, Mem. New York Bot. Gard. 1:50. 1900. Based on *P. flexuosa* var. *occidentalis* Vasey, 1878.

Poa lacustris Heller, Muhlenbergia. 6:12. 1910. Based on *P. flexuosa* var. *occidentalis* Vasey, 1878.

Perennial, commonly blue-green and often variously anthocyanic, with or without short rhizomes; culms erect to 125 cm tall, glabrous or with some retrorse scabrosity about the nodes; sheaths mostly shorter than the internodes, rarely closed less than 50% of their length, strongly keeled, glabrous or less commonly strongly retrorsely scabrous, rarely retrorsely puberulent; ligules obtuse to acute, often apiculate, glabrous to strongly pubescent on the abaxial surface, ligules of the upper leaves to 4.5 mm long, usually shorter than the leaf width; blades mostly cauline, strongly keeled, flat, rarely folded except when young, prominently prow-tipped, the upper ones usually the longest, 6–18 cm long, 2–5.5 mm wide; panicle narrowly to broadly pyramidal, (8-) 13–29 cm long, erect, the lower internodes elongate, branches 1–5 per node, divergent when young, widely spreading to reflexed when mature, the longest 2.5–18 cm long, with 4–34 spikelets; spikelets mostly on the distal 1/2 of the branches, 3–8 mm long, with 1–8 florets, oblong, usually longer than the subtending pedicels, the rachilla usually

visible; glumes narrow, acute, the first usually less than 1/2 the length of the first lemma, 1-nerved, 1.6–3.5 mm long, the second usually slightly shorter than the first lemma, 1–3-nerved, 2.2–4.4 mm long; lemmas green, strongly keeled, with whitish, scarious acute tips, the first 2.6–5 mm long, cobwebby hairs from the callus long and abundant or rarely nearly absent, usually with long, villous pubescence on the lower 3/4 to 1/2 of the keel, and 1/2 to 1/3 of the marginal nerves, usually puberulent between the nerves on the lower 1/2, the intermediate nerves usually indistinct; paleas usually minutely scabrous on the nerves (pilose in one specimen), 2/3 to nearly equaling the lemma in length; flowers perfect or imperfect, the two types usually mixed in the same inflorescence, sometimes all one or the other, the imperfect ones usually with aborted anther sacs present, the developed anthers 1.25–3 mm long.

Southern Rocky Mts., in the Park, Sawache, and Front ranges, Sangre De Cristo, and White mountains of Colorado, and in the San Juan, Sangre De Cristo, Sandia, White, and Sacramento mountains of New Mexico. Flowering from May to mid-July over most of its range, mid-July to mid-August in the White and Sacramento mountains of southern New Mexico. In humus rich soils, in thickets and forest openings, elevation 2000–3500 m.

Hitchcock (1935), Keck (1964), Beetle (1977), and Dorn (1977) have indicated that *P. tracyi*, or, *P. occidentalis* occurs in Wyoming. These distribution records appear to be based on three collections: *Buffum* 4907; *Buffum* 5111; and *Beetle* 1064. Although none of the above collections represent *P. tracyi*, or *P. occidentalis*, *P. tracyi* may yet be found there in the Big Snowy Range.

Poa tracyi has the strongly pubescent and webbed, narrow lemmas, long relatively broad blades, long panicles, stature, and tolerance of dry (relative to other members of this complex) habitats that are typical of *P. occidentalis*. However, *P. tracyi* has long anthers (when these are developed), short and often pubescent ligules, sheaths that are occasionally pubescent, and are closed most of their length, few flowered panicle branches, and occasional rhizomes, all characters that are typical of *P. nervosa* (Hook.) Vasey (especially in the *P. wheeleri* Vasey form). *Poa tracyi* it seems is intermediate between these species. *Poa tracyi* is perhaps more closely allied to the more western *P. curta sensu auct.* (there being some question about the identity of the type), a species similar in nearly all respects, but lacking floral or vegetative pubescence. *Poa tracyi* shows affinities to *P. reflexa* and *P. leptocoma*, and in some specimens is clearly distinguished from these only by its markedly longer anthers.

Keck suggested two subspecies (described and assigned types in an unpublished manuscript, and annotated specimens) of *P. tracyi*, neither of which is formally recognized here. His unpublished subsp. *durangoensis* appears to be conspecific with *P. aperta* Scribn. & Merr., a species quite distinct from *P. tracyi*. The unpublished subsp. *oterensis*, was segregated

on the basis of plants from the White and Sacramento mountains that had scabrous to pubescent sheaths. Because the presence of these characters appears to be highly variable in *P. tracyi* from this region, and many individuals from there are morphologically identical material to *P. tracyi* from Raton, New Mexico, the type locality, this segregation seems undesirable.

ACKNOWLEDGEMENTS

Authors wish to acknowledge the encouragement and help of Kelly Allred, the morphometric analyses suggestions by John Ludwig, and the guidance, comments and critical review of Richard Spellenberg. The efforts of the curators of herbaria (ARIZ, BH, BRY, CAN, CAS, CSU, CU, COLO, DAO, GH, MO, NMC, NY, POM, RM, RSA, TAES, UC, UNM, US, UT, UTC, and V) supplying loans for this project were sincerely appreciated.

REFERENCES

- ABRAMS, L. 1940. Illustrated flora of the Pacific States, vol. 1. Stanford Univ. Press.
- BARR, A. J., J. H. GOODNIGHT, J. P. SMALL and J. T. HELWIG. 1976. A user's guide to SAS 76. Raleigh, N. C.: SAS Institute.
- BEEBLE, A. A. 1977. Grasses of Wyoming. Univ. Agric. Exp. Sta. Res. J. 39R. 154 pp.
- CAVE, M. S. ed. 1964. Index to plant chromosome numbers for 1963. Chapel Hill: Univ. of North Carolina Press.
- CRUDEN, R. W. 1977. Pollen-ovule ratios: A conservative indicator of breeding systems in flowering plants. *Evolution*. 31:32-46.
- DIXON, W. J. 1975. Biomedical computer programs. Berkeley: Univ. California Press.
- DORN, R. D. 1977. Manual of the vascular plants of Wyoming, vol. 2. New York: Garland Productions Inc.
- FEDOROV, A. A. 1969. Chromosome numbers of flowering plants. Acad. Sci. U.S.S.R., Leningrad: Komarov Botanical Institute.
- GOLDBLATT, P. ed. 1981. Index to plant chromosome numbers 1975-1978. Missouri Bot. Gard.: Monogr. Syst. Bot. vol. 5.
- HARRINGTON, D. H. 1954. Manual of the plants of Colorado. Denver: Sage Books.
- HATCH, S. L. 1980. Chromosome numbers of some grasses from the southwestern United States and Mexico. *Southw. Naturalist* 25:278-280.
- HITCHCOCK, A. S. 1935. Manual of the grasses of the United States. U.S.D.A. Misc. Pub. 200. U.S. Govt. Print. Off.
- HOWELL, T. 1903. A flora of Northwest America, vol. 1, fascicle 7. Portland: Privately published.
- HULTEN, E. 1968. Flora of Alaska and neighboring territories. Stanford: Stanford Univ. Press.
- KECK, D. D. 1964. *Poa*. Pp. 17-21 in, A flora of Wyoming, part 3, by C. L. Porter. Univ. Agric. Exp. Sta. Bull. 418.
- McLAUGHLIN, S. and C. T. MASON Jr. 1977. Notes on new and rare Arizona plants. *J. Arizona Acad. Sci.* 12:203-204.
- MARSH, V. L. 1950. A taxonomic revision of the genus *Poa* of the United States and southern Canada. Ph.D. Thesis, Univ. Washington.
- MARTIN, W. C. and C. R. HUTCHINS. 1980. A flora of New Mexico, vol. 1. Germany: J. Cramer.
- MAYR, E. 1969. Principles of systematic zoology. New York: McGraw Hill.

- MOORE, R. J. ed. 1973. Index to plant chromosome numbers 1967-1971. *Regnum Veg.* 90:1-539.
- . 1977. Index to plant chromosome numbers for 1973/74. *Regnum Veg.* 96:1-257.
- RYDBERG, P. A. 1922. *Flora of the Rocky Mountains and adjacent plains*. New York: Hafner Publishing Co.
- SCOGGAN, H. J. 1978. The flora of Canada. *Natl. Mus. Natur. Sci. Pub. Bot.* No. 7(2):315.
- SNOW, R. 1963. Alcoholic hydrochloric acid-carmines as a stain for chromosomes in squash preparations. *Stain Technol.* 38:413.
- SORENG, R. J. 1980. A biosystematical comparison of *Poa occidentalis* Vasey and *Poa tracyi* Vasey. MS Thesis. New Mexico State Univ.
- TRACY, S. M. 1888. Report of an investigation of the grasses of the arid districts of Texas, New Mexico, Arizona, Nevada, and Utah, in 1887. Washington D. C.: U. S. Govt. Print. Off. Jan. 20.
- WEBER, W. A. and B. C. JOHNSTON. 1979. Natural history inventory of Colorado, part 1. 2nd. ed. Boulder: Univ. of Colorado Museum.
- WOOTON, E. O. and P. C. STANDLEY. 1913. The grasses and grass like plants of New Mexico. Las Cruces: New Mexico Coll. Agric. and Mech. Arts. Agric. Exp. Sta. Rio Grande Republican.